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Miocene Amphicyonids (Mammalia, Carnivora) from the Agate Spring Quarries, Sioux County, Nebraska

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ABSTRACT

The Miocene late Arikareean land mammal "age" is largely defined by the faunal assemblage from the Agate Spring Quarries and other nearby localities in the Harrison Formation of Sioux County, Nebraska. Amphicyonid carnivores of the genera *Cynelos* Jourdan and *Ysengrinia* Ginsburg were previously known only from European Oligocene and Miocene deposits. These genera are now known from the Harrison Formation of Sioux and Box Butte counties, western Nebraska, and therefore the late Arikareean fauna now includes three amphicyonids: *Cynelos* sp., (?) *Ysengrinia* sp., *Daphoenodon superbus* Peterson. The stage of evolution of these carnivores suggests a correlation of the Agate Spring Quarries fauna with early to medial Aquitanian faunas of western Europe.

INTRODUCTION

Mid-Tertiary amphicyonid carnivores are potentially useful in biostratigraphic correlation of European and North American rock units. Several genera and probably some species have extensive geographic distributions spanning these continents coupled with relatively short temporal ranges. Morphologically diverse amphicyonid species occupied a broad range of ecological niches and included forms that paralleled ursids and canids in dental and postcranial anatomy.

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While engaged in a study of North American amphicyonids, I had the opportunity to examine the early Miocene fossil carnivores from the Agate Spring Quarries that were collected for the Carnegie Museum between 1904 and 1909 by O. A. Peterson. The late Arikareean faunal assemblage from the quarries included three species: the amphicyonid¹ *Daphoenodon superbus* Peterson, the canid *Nothocyon annectens* Peterson, and the mustelid *Paroligobunis simplicidens* Peterson. The canid and mustelid are known from the remains of single individuals which were found together with several almost complete skeletons of the amphicyonid in Agate Spring Quarry 3.²

Since then, no other carnivores have been described from the quarries. However, during re-examination of Peterson's material, an unusual lower carnassial from Agate Spring Quarry 1 could not be referred to *Daphoenodon superbus* because of its small size and distinctive morphology. This tooth is most similar to lower carnassials of the European amphicyonid genus *Cynelos* Jourdan. Shortly thereafter, I had occasion to examine a humerus, calcaneum, and fifth metacarpal which Peterson had described in 1910 as an indeterminate canid of large size. Humerus and calcaneum had been found in the Harrison Formation within a few miles of the Agate Spring Quarries, and the metacarpal was one of the first bones found at the site of the University of Nebraska Quarry on University Hill which later was to produce a large part of the classic Agate Spring Quarries faunal assemblage. These postcranial bones belong to a large bearlike amphicyonid, rather than a canid. Generic affinities are uncertain. On the basis of Peterson's three postcranial bones and additional material discovered by field parties of the Frick Laboratory of the American Museum of Natural History, it appears to be closely related to the European deep-jawed amphicyonids placed in the genera *Brachycyon* Filhol, *Ysengrinia* Ginsburg, and *Pseudocyon* Lartet. I tentatively refer the material to (?) *Ysengrinia*.

¹ Amphicyonidae Trouessart, 1885, is regarded here as a family of fissiped carnivores distinct from the Canidae of Gray, 1821 (Hunt, MS). The term was first proposed by Trouessart as a subfamily of the Canidae.

² In his monograph on the fossil carnivores of the Agate Spring Quarries, Peterson (1910, p. 206) reported that "Scattered remains of a number of individuals [of the amphicyonid *D. superbus*], apparently of the same species, were found in all of the Agate Spring Fossil Quarries, but in Quarry No. 3 were found the most abundant remains . . . Besides the type of *Nothocyon annectens* Peterson and [the mustelid *Paroligobunis*] there was little else found in Quarry No. 3 except remains of *Daphoenodon superbus*." This single paper by Peterson on the carnivores contrasts with a rather extensive literature on the more abundantly represented ungulates (e.g., Peterson, 1906, 1909, 1920; Holland and Peterson, 1914), reflecting the rarity of carnivores in these quarries.

ACKNOWLEDGMENTS

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ABBREVIATIONS

AMNH, the American Museum of Natural History

CM, Carnegie Museum

FMNH, Field Museum of Natural History

F:AM, Frick Collection, the American Museum of Natural History

THE AGATE SPRING QUARRIES

Figures 1-5

During the summer of 1904, while working in western Nebraska in the employ of the Carnegie Museum, O. A. Peterson opened the first of several excavations in the Harrison Formation of Sioux County which became known as the Agate Spring Quarries. The quarries are situated about 1/2 mile south of the Niobrara River and about 3 miles east of the former postoffice of Agate in SW 1/4, NE 1/4, sect. 10, T. 28 N, R. 55 W, Whistle Creek 1:125,000 topographic quadrangle. The quarries are situated in a group of four low hills of which two (Carnegie Hill, University Hill) are larger and more prominent and have produced the greater quantity of fossil material. A brief account of early work in the quarries is given by Holland and Peterson (1914).

The first quarry opened by Peterson was designated "Quarry A." It was worked on a relatively small scale in 1904, in comparison to later excavations on the nearby larger hills, yielding a small quantity of rhinoceros, horse, and chalicothere bones.¹ Toward the end of the summer on August 9, 1904, the day before he returned to the East because of ill

¹ This and subsequent statements are based on Peterson's field labels of 1904 in the Carnegie Museum.

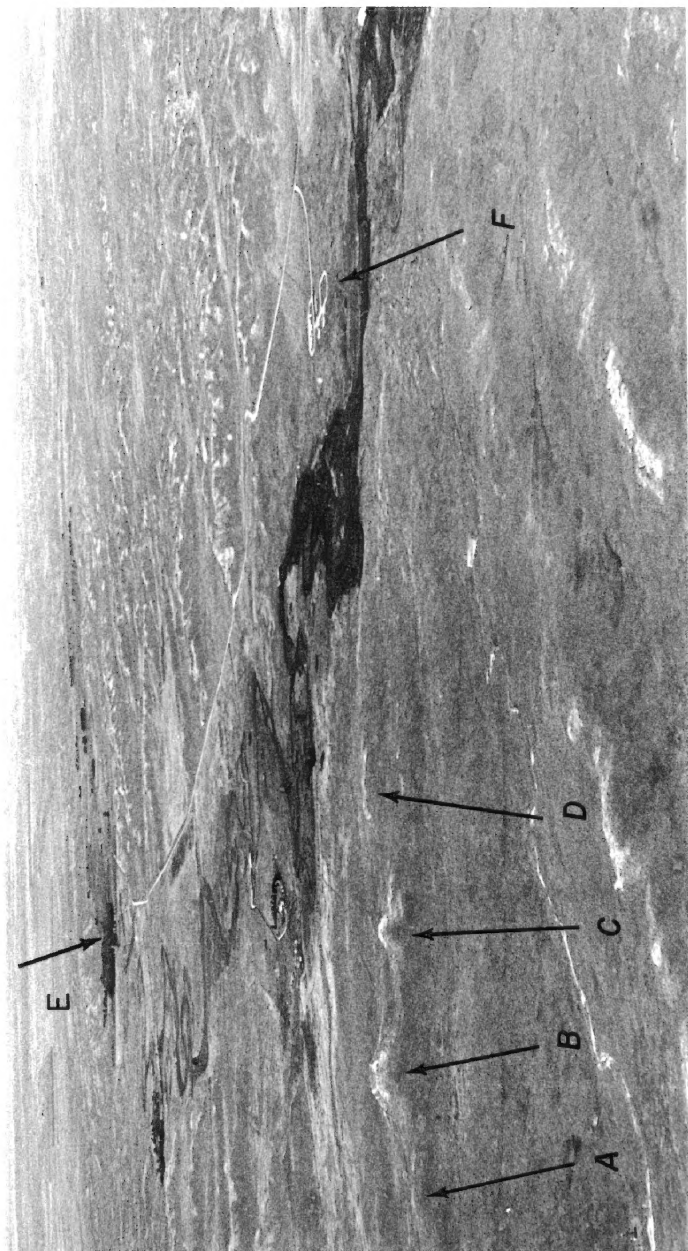


FIG. 1. High oblique aerial photograph of Agate Spring Quarries, Sioux County, Nebraska, looking west along the course of the Niobrara River. A. Quarry 3. B. Carnegie Hill (Quarry 1). C. University Hill (University of Nebraska Quarry). D. Quarry A. E. Agate postoffice and Cook homestead. F. Headquarters, Agate Spring Quarries National Monument.

health, Peterson explored Carnegie Hill and University Hill approximately 100 yards south of Quarry A and collected a few bones from the surface talus.¹ Peterson realized that the bone-bearing rock stratum present in the small hill containing Quarry A was also present in the two prominent hills, justifying plans for an extensive program of excavation in subsequent field seasons. During the next decade, quarries in Carnegie Hill and University Hill produced the greater part of the classic Agate Spring Quarries faunal assemblage. Field parties from numerous institutions worked the quarries: the University of Nebraska, the Carnegie Museum, the American Museum of Natural History, Amherst College, and Yale University.

About 50 yards south of Carnegie Hill is a small unnamed hill in which is situated Quarry 3, the source of Peterson's three carnivore species. Apparently Quarry 3 was discovered in 1904 as were the potential sites on Carnegie and University hills (Peterson, 1910, p. 205). It was not worked until the summer of 1905 at which time the amphicyonid sample as well as the canid and the mustelid were collected.

The current concept of the late Arikareean age is based almost entirely on the Agate Spring Quarries faunal assemblage, that is, on specimens obtained from Carnegie Hill, University Hill, and from Quarry A and Quarry 3, and on specimens from a few other sites in the immediate area. Thus the presence of two new amphicyonids in these quarries indicates that they were an integral part of the late Arikareean fauna, expanding the number of known carnivore species to five: three amphicyonids, a canid, and a mustelid.

However, only M_1 of *Cynelos* and a metapodial of (?) *Ysengrinia* have been found at the Agate Spring Quarries. Identification and supplementary knowledge of these carnivores has been possible by assembling additional fragmentary remains from other nearby quarries in the Harrison Formation of western Nebraska. The following specimens constitute the basis of the present report:

- (1) Agate Spring Quarry 1, Carnegie Hill, Sioux County—isolated M_1 (CM 2200), *Cynelos* sp.
- (2) University of Nebraska Quarry, University Hill, Sioux County—metacarpal V (CM 1897), (?) *Ysengrinia* sp.
- (3) Morava Ranch Quarry, NE 1/4, sect. 6, T. 28 N, R. 52 W, Box Butte County—edentulous lower jaw (F:AM 25423), distal humerus (F:AM

¹ Only an anterior lower jaw fragment of *Daphoenodon superbus* (CM 1896g) and a metapodial of (?) *Ysengrinia* (CM 1897) were collected at that time, according to 1904 field labels.

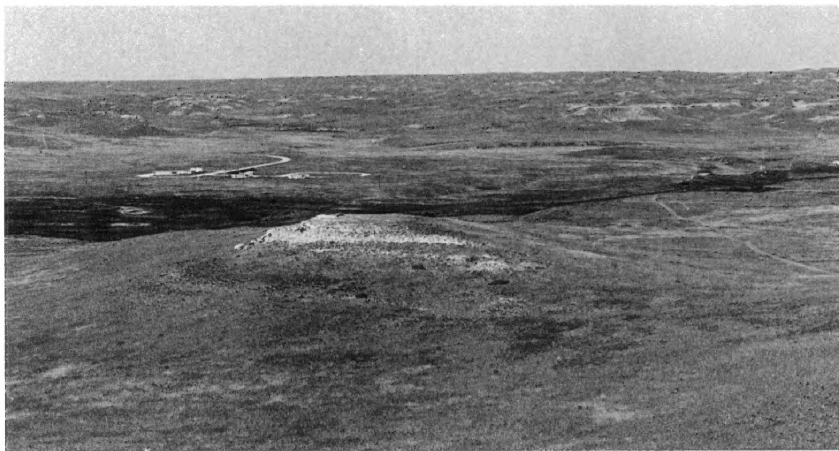


FIG. 2. Quarry A, site of Peterson's original excavation, with National Monument headquarters in background to the north. Peterson's quarry level apparently was situated in the west face of the hill. The dissected low hills north of Niobrara River are formed by the Harrison Formation overlain by the "Upper Harrison" beds of Peterson.

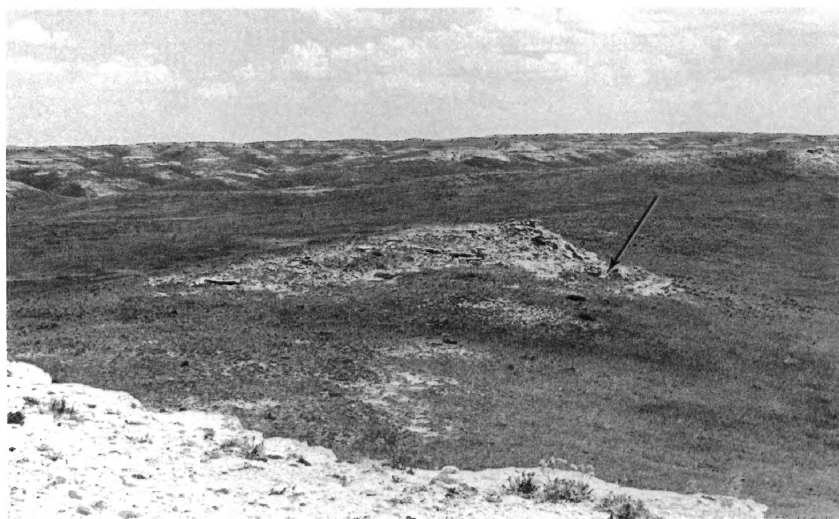


FIG. 3. Small, unnamed hill containing Peterson's Quarry 3 about 50 yards south of Carnegie Hill. Flat, light-colored surface in foreground is the "Agate Lime," a siliceous carbonate ledge about 1 to 2 feet thick capping Carnegie Hill. Bone was found at two levels on west face of hill either of which could have been the site of Peterson's excavations. Arrow indicates location at which a partial humerus of *Daphoenodon superbis* was found in 1971.



FIG. 4. Looking northeast at University Hill and University of Nebraska Quarry. Level of University of Nebraska Quarry is indicated by path along face of hill. Niobrara River can be seen beyond hill.



FIG. 5. Quarry 1 on west face of Carnegie Hill. Now under excavation by the National Parks Service, the original quarry level cannot be seen, but lies slightly below the flat on which scraper sits. Note laminated and cross-bedded fluvial sediments above quarry; such fluvial deposits characterize all the Agate Spring Quarries.

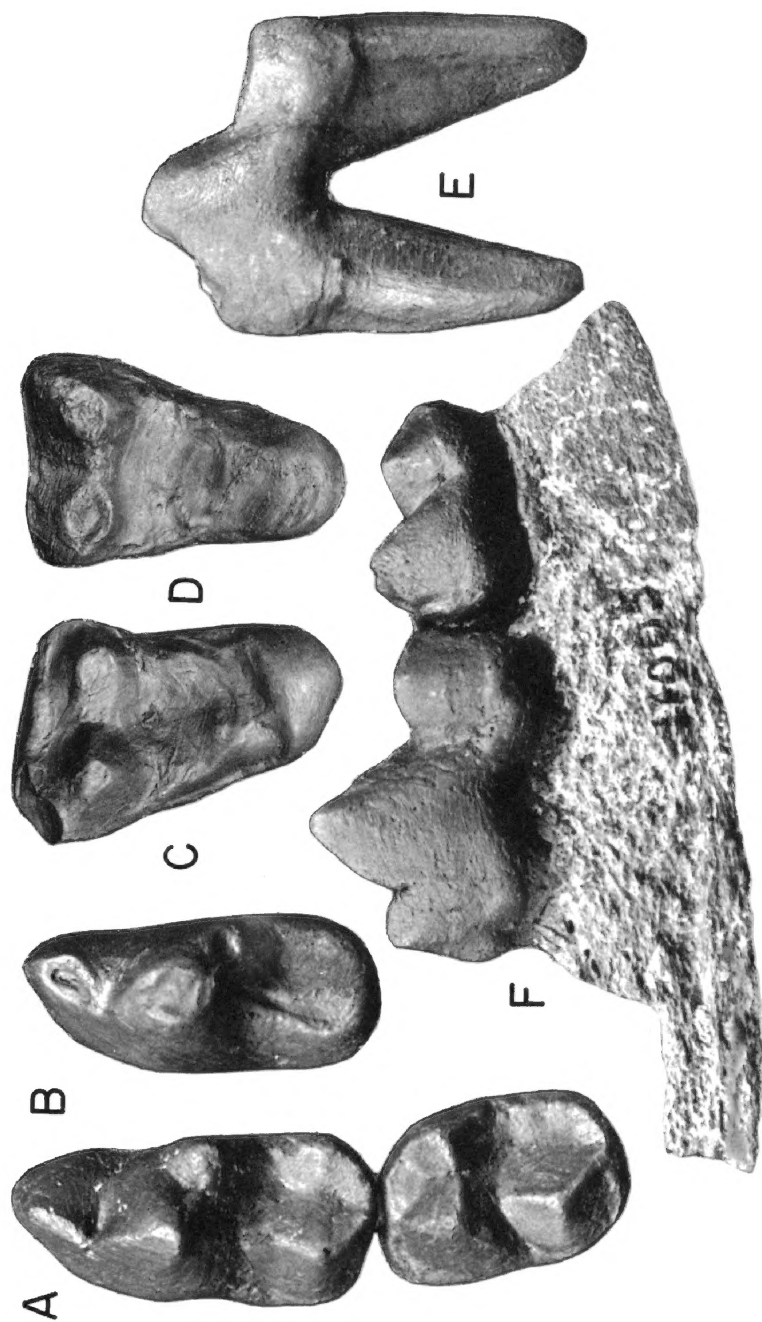


FIG. 6. A. AMNH 11005, *Cynelos lemanensis*, St.-Gerand-le-Puy, occlusal view of M_1 -2. B. CM 2200, *Cynelos* sp., Agate Spring Quarry 1, occlusal view of M_1 . C. AMNH 11008, *Cynelos lemanensis*, Peu-Blanc, occlusal view of M^1 . D. AMNH 81054, *Cynelos* sp., American Museum-Cook Quarry, occlusal view of M^1 . E. Same as B, lateral view. F. Same as A, lateral view. All $\times 2.0$.

- 25421), M¹ (F:AM 25420), phalanx (F:AM 25433), (?) *Ysengrinia* sp., and proximal radius (F:AM 25434), (?) *Cynelos* sp.
- (4) Quarry, exact location unknown, situated according to Peterson on Whistle Creek, about 8–10 miles east of the Agate Spring Quarries, Sioux County—complete humerus (CM 2400), (?) *Ysengrinia* sp.
- (5) American Museum-Cook Quarry,¹ 2 miles north of the Agate Spring Quarries, Sioux County—calcaneum (CM 2211) and M¹ (AMNH 81049), (?) *Ysengrinia* sp., and isolated M¹ (AMNH 81051), *Cynelos* sp.

Cynelos sp.

Figures 6, 7

DESCRIPTION: *Cynelos* is represented by an isolated water-worn lower carnassial (CM 2200) from Agate Spring Quarry 1, Carnegie Hill, collected in 1908 by Peterson who identified it as "*Amphicyon* sp." It measures 21.3 mm. in greatest length, 9.3 mm. in width at the posterior border of the trigonid, and is narrower and shorter than lower carnassials of *D. superbus* (table 1). The trigonid and talonid lengths of M₁ from Quarry 1 are approximately the same. The paraconid is anterior and slightly medial to the protoconid with the metaconid half the distance up the postero-medial protoconid slope. The posterior slope of the protoconid descends gradually to meet the ascending talonid surface. An elliptical depression, a remnant of an elongate hypoconid, occupies the lateral talonid rim. Only a slight swelling of the medial talonid rim indicates the region of the worn entoconid ridge. Cusps as well as the remainder of the tooth surface have been worn smooth, so that some original relief has been lost; however, evidence of a cingulum is not present and probably was absent from the unworn tooth, judging from European carnassials of this genus.

A worn M¹ (AMNH 81051) from the American Museum-Cook Quarry corresponds in size to the M₁ from Quarry 1. It was collected in July, 1908, by Harold Cook of Agate, Nebraska. This tooth differs in size and form from the larger more robust first upper molars of *D. superbus* found in the same quarry (table 2). Most striking is the short length relative to great transverse width, presenting the form of an isosceles rather than an equilateral triangle in occlusal view. The concave appearance of the tooth is due to the depressed protocone basin. Internal to the basin is the worn protocone rising from the anteromedial border. A pronounced shelflike cingulum surrounds the protocone both posteriorly and medially. Anteriorly, the cingulum is thin but distinct, whereas posteriorly it blends with

¹ See Addendum.



FIG. 7. Proximal radii of *Daphoenodon superbus* (CM 2774), left, Quarry 3, Sioux County, Nebraska, and *Cynelos* sp., (F:AM 25434), right, Morava Ranch Quarry, Box Butte County, Nebraska. $\times 1.0$.

the posterior border of the tooth. The cingulum is not prominent laterally near the metacone but thickens to a small parastyle beside the paracone. Weak intermediate cusps lie at the bases of paracone and metacone where

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF M_1 OF *Cynelos* SP. AND *Daphoenodon superbus*
FROM THE HARRISON FORMATION OF WESTERN NEBRASKA

			Length ^a	Width ^b	Locality
<i>Cynelos</i> sp.	CM	2200	21.3	9.3	Quarry 1
<i>D. superbus</i>	CM	1589	24.2	11.6	Quarry 3
	CM	1589A	26.2	11.2	Quarry 3
	CM	1589D	25.9	11.6	Quarry 3
	CM	2774	24.2	11.1	Quarry 3
	CM	2217	26.5	11.5	?AMNH-Cook
	AMNH	81003	25.2	10.8	AMNH-Cook
	AMNH	81025	27.4	11.2	AMNH-Cook
	F:AM	54460	26.4	11.7	Harris Ranch
	FMNH	P12033	26.1	11.3	Sioux County

^a Greatest length from anterior paraconid border to posterolateral corner of talonid.

^b Greatest width across posterior trigonid.

the ridges leading laterally from the protocone contact these cusps.

A proximal left radius (F:AM 25434) from Morava Ranch Quarry is tentatively referred to *Cynelos* (fig. 7). Size of the bone indicates an animal smaller than individuals of *D. superbus*. Length of the radial fragment from the capitular eminence to the broken distal border is about 62 mm.; greatest width of the radial head is 24.3 mm. The articular surface of the radial head is not flat as in *Daphoenodon* Peterson but rather has a spiral configuration such that the surface rises in height from the lateral to the medial border. The spiral configuration is significant in the interpretation of the orientation of the elbow joint.

The radial tuberosity for the tendon of the biceps muscle is an elliptical protuberance on the posterior surface. It lies more toward the lateral edge of the bone and is incised by a dorsoventrally placed groove. On the anterior face of the radius opposite the radial tuberosity is another elevation for the lateral collateral ligament of the elbow joint situated toward the lateral side of the anterior surface. It measures about 6 by 8 mm., whereas the radial tuberosity measures 10 by 16 mm. In *D. superbus* (CM 2774, 1589B), there is a deep elliptical scar proximal to the radial tuberosity which is absent in the radius from the Morava Ranch Quarry.

DISCUSSION: Species of *Cynelos* are reported from eleven localities in Europe: (1) fissure fillings, Phosphorites du Quercy, France, *C. crassidens* (Filhol), *C. piveteaui* Ginsburg (?Sannoisian to ?medial Stampian); (2) St.-Henry, France, *C. crassidens* (medial Stampian); (3) Peu-Blanc, France, *C. lemanensis* (Pomel) (early Aquitanian); (4) Paulhiac, France, *C. lem-*

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF M¹ OF *Cynelos* SP., *Daphoenodon superbus*, AND
(?)*Ysengrinia* SP. FROM THE HARRISON FORMATION OF WESTERN NEBRASKA

			Length ^a	Width ^b	Quarry
<i>Cynelos</i> sp.	AMNH	81051	13.2	21	AMNH-Cook
<i>D. superbus</i>	AMNH	81050	17.1	23.9	AMNH-Cook
	CM	2774	18.0	24.0	Quarry 3
	AMNH	81055	18.1	23.6	AMNH-Cook
	AMNH	81048	18.9	26.6	AMNH-Cook
	CM	1589A	19.0	25.3	Quarry 3
(?) <i>Ysengrinia</i> sp.	AMNH	81049	19.8	26.5	AMNH-Cook
	F:AM	25420	21.1	30.2	Morava Ranch

^a Greatest length measured across paracone and metacone.

^b Greatest width measured from anterolateral corner to most medial part of protocone cingulum.

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF M_1 OF EUROPEAN SPECIES OF *Cynelos*
FROM STAMPIAN, AQUITANIAN, AND BURDIGALIAN DEPOSITS

	Length	Width	Locality
<i>Cynelos crassidens</i>			
Ginsburg, 1966, p. 15	17	8.9	Phosphorites du Quercy
Ginsburg, 1966, p. 15	16.8	8.4	St.-Henry
Ginsburg, 1966, p. 15	16.7	7.9	St.-Henry
<i>Cynelos piveteaui</i>			
Ginsburg, 1966, p. 13	21.5	10.4	Phosphorites du Quercy
<i>Cynelos lemanensis</i>			
Kuss, 1965, p. 57	22	—	Ulm
Viret, 1929, p. 109	20.5	—	St.-Gerand
Viret, 1929, p. 112	19	—	St.-Gerand
Viret, 1929, p. 112	19.8	—	St.-Gerand
AMNH 11005	21.9	10	St.-Gerand
<i>Cynelos rugosidens</i>			
Kuss, 1965, p. 63	19.5	8.8	Ulm
Viret, 1929, p. 116	17.3	8	St.-Gerand
Kuss, 1965, p. 63	17.7	8	?St.-Gerand
AMNH 11004	18	7.9	St.-Gerand
<i>Cynelos helbingi</i>			
Dehm, 1950, p. 25	19.8–27.1 ^a	9.2–11.3 ^b	Wintershof-West
<i>Cynelos schlosseri</i>			
Dehm, 1950, p. 17	15.9–18 ^c	6.8–8.1 ^c	Wintershof-West

^a N = 23.

^b N = 4.

^c N = 10.

anensis (early Aquitanian); (5) Pyrimont-Challonges, Switzerland, *C. lemanensis* (early Aquitanian); (6) St.-Gerand, Montaigu, France, *C. lemanensis*, *C. rugosidens* (Schlosser) (medial Aquitanian); (7) Weisenau (Mainz Basin), Eckinggen and Haslach (near Ulm), Germany, *C. lemanensis*, *C. rugosidens* (medial to late Aquitanian); (8) Laugnac, France, *C. lemanensis*, *C. rugosidens* (late Aquitanian); (9) Cetina de Aragón, Spain, *C. lemanensis* (late Aquitanian); (10) fissure fillings, Wintershof-West, near Eichstätt, Bavaria, *C. helbingi* (Dehm), *C. schlosseri* (Dehm) (early Burdigalian); (11) Anjou marls, Loire Basin, France, *C. sp.* (early Helvetian).

Lower carnassials of *Cynelos* (AMNH 11004, 11005) in the collections of the American Museum from the medial Aquitanian of St.-Gerand-le-Puy, France, compare well with M_1 from Quarry 1 (fig. 6A, B, E, F). Among European species, the Quarry 1 carnassial corresponds in size to

TABLE 4
MEASUREMENTS (IN MILLIMETERS) OF M¹ OF EUROPEAN SPECIES OF *Cynelos*
FROM STAMPIAN, AQUITANIAN, AND BURDIGALIAN DEPOSITS

	Length	Width	Locality
<i>Cynelos crassidens</i>			
Ginsburg, 1966, p. 15	13.4	17.6	St.-Henry
Ginsburg, 1966, p. 15	10.8	17.9	St.-Henry
<i>Cynelos piveteaui</i>			
Ginsburg, 1966, p. 13	15.9	19.5	Phosphorites du Quercy
<i>Cynelos lemanensis</i>			
Viret, 1929, p. 111	13	18	?St.-Gerand
Viret, 1929, p. 111	13.5	17	Montaigu-le-Blin
Viret, 1929, p. 111	15	19.5	St.-Gerand
Viret, 1929, p. 111	16	19	?St.-Gerand
Kuss, 1965, p. 57	14.2	21.8	Peu-Blanc
<i>Cynelos rugosidens</i>			
Kuss, 1965, p. 63	14.5	17.5	Ulm (Haslach)
<i>Cynelos helbingi</i>			
Dehm, 1950, p. 25	15.6–20.8 ^a	19.2–25.2 ^a	Wintershof-West
<i>Cynelos schlosseri</i>			
Dehm, 1950, p. 27	12.0–13.2 ^b	15.8–17.7 ^b	Wintershof-West

^a N = 19.

^b N = 6.

lower carnassials of *C. helbingi* and *C. lemanensis* but not to those of *C. rugosidens*, *C. schlosseri*, or *C. crassidens* (table 3).

The worn M¹ from the American Museum-Cook Quarry combines short length with a rather considerable transverse width, dimensions which exclude the possibility of referral to *C. helbingi*, *C. schlosseri*, *C. crassidens*, and *C. piveteaui* (table 4). Likewise, the dimensions of M¹ in *C. rugosidens* suggest a transversely short tooth, although few specimens are known.

The most satisfactory comparison is with an M¹ (AMNH 11008) attributed to *Cynelos lemanensis* from early Aquitanian deposits at Peu-Blanc, France (fig. 6C, D). Both teeth share a similar cusp pattern as well as a marked transverse width relative to short length. Both have a pronounced swollen internal cingulum posteromedial to the protocone. The slight differences that exist between the two molars can be attributed to the worn condition of AMNH 81051.

Recently Ginsburg and Telles-Antunes (1968, p. 24) implied that a third species from Wintershof-West can be included in *Cynelos*. Originally described by Dehm (1950, p. 30) as *Amphicyon dietrichi*, this species is con-

sidered by Ginsburg and Telles-Antunes as "la forme la plus extrême de la variation individuelle" of *C. helbingi*. M_1 of *C. dietrichi* measures 29 by 12.8 mm. whereas M^1 measures 22.1 by 27.8 mm., indicating a large amphicyonid. *Cynelos* from Nebraska can be excluded from this species.

Early Helvetian *Cynelos* reported by Ginsburg (1970, p. 189) from the Anjou marls of the Loire Basin at present remain undescribed. These would be the youngest specimens referred to the genus and are probably large carnivores.

M_1 (CM 2200) from Quarry 1 and M^1 (AMNH 81051) from the American Museum-Cook Quarry are the only known teeth of *Cynelos* in the Harrison Formation. The Quarry 1 carnassial falls within the size range of *C. helbingi* and *C. lemanensis*, but a lower carnassial is not sufficiently diagnostic to distinguish between these two species. However, if the M^1 from the American Museum-Cook Quarry is considered to belong to the same species as the Quarry 1 M_1 , then *C. helbingi* can be ruled out because it has a more massive M^1 . The North American material thus compares most satisfactorily with teeth of *Cynelos lemanensis*.

No additional taxonomic information is gained from the radius. Lack of associated postcranial and dental material in Europe has produced an amphicyonid taxonomy based chiefly on the teeth. However, the spiral configuration of the radial head demonstrates that this amphicyonid had a greater angle between the long axis of humerus and radius than did *Daphoenodon*. This in turn indicates that the elbow joint in *Cynelos* was angled outward in the frontal plane, more so than in *Daphoenodon*. In mammals in which the long axis of the radius and the humerus are approximately parallel, the radial head will have a uniformly concave surface of equal height on both lateral and medial borders. However, in mammals such as ursids in which the radius lies at an angle to the humerus, the surface of the radial head takes a spiral configuration. The surface of the radius which articulates with the capitulum of the humerus lies at a greater angle to the radial shaft in order to maintain a tight articulation with the humerus. In the fully supinated position, the radius is longer, so to speak, than in the fully pronated position because the radial shaft crosses over the ulna during pronation and becomes effectively shorter. By the spiral configuration of the radial head, this change in effective length is compensated. Movement on the spiral is upward from the supinated position to the pronated position, thus the increase in effective length of the bone gained by the spiral articulation makes up for the effective length lost by the change in position from the supinated to the pronated radius.

(?) *Ysengrinia*

Figures 8-14

DESCRIPTION: An edentulous lower jaw (F:AM 25423) of a large amphicyonid was collected by Ted Galusha in 1940 from the Harrison Formation, Morava Ranch Quarry, NE 1/4, sect. 6, T. 28 N, R. 52 W, Box Butte County, Nebraska (figs. 8, 9). The jaw is particularly massive, thick, and deep in its anterior part in contrast to the slender wolflike jaws of *Daphoenodon superbus* and *Cynelos*. The jaw measures 56 mm. in depth below the talonid of M_1 , about 51 mm. in depth below the anterior root of P_2 . There is no premasseteric fossa developed in the lateral face of the horizontal ramus as in hemicyonine ursids.

Measurements of the alveolar length of the lower teeth are: $P_1 = 6.7$ mm., $P_2 = 14.1$ mm., $P_3 = 17.0$ mm., $P_4 = 19.4$ mm., $M_1 = 32.6$ mm., $M_2 = 20$ mm., $M_3 = ?$ (alveolus present but eroded). The length of the tooth row measured as the distance from the posterior alveolar border of the canine to the posterior border of M_2 alveolus is 123 mm. Length of the premolar row measured from the anterior border of P_1 alveolus to the posterior border of P_4 alveolus is 62.1 mm.

P_1 was a single-rooted tooth, separated by a short diastema (3.5 mm.) from a double-rooted P_2 . Probably only a short diastema was present between P_2 and P_3 . From the position of the alveoli, P_3 was elongate, double rooted, and placed near P_4 . P_4 itself was sandwiched tightly between P_3 and M_1 . From the form of M_1 alveolus, the trigonid of M_1 was longer than the talonid. M_2 apparently was short relative to M_1 (M_1/M_2 alveolar length ratio = 1.63). M_3 appears to be single rooted but since the alveolus is eroded, this is not certain. The canine alveolus was massive and deep, somewhat laterally compressed, indicating a large root.

An unworn M^1 (F:AM 25420) from the Morava Ranch Quarry (fig. 10A) measures 21.1 mm. in length and 30.2 mm. in greatest transverse width, indicating a larger tooth than found in any known *D. superbus* (table 2). The dominant feature is the prominent paracone and metacone, the former larger than the latter. They are bordered laterally by a weak cingulum. Two low ridges without accessory cusps lead from the respective bases of the paracone and metacone to the relatively low, V-shaped protocone which is tilted upward at its tip when seen in occlusal view. Medial to the protocone appears a prominent cingular shelf, much more developed posteromedially and medially; it is virtually absent anteriorly and on the lateral half of the posterior border of M^1 . A slightly smaller M^1 (AMNH 81049) of (?) *Ysengrinia* was found in the American Museum-Cook Quarry by Harold Cook in July, 1908 (fig. 10B). These teeth are

similar to the type specimen (M^1) of *Amphicyon intermedius* Von Meyer from the medial Aquitanian Süsswasserkalk of Michelsberg near Ulm, Germany (Stuttgart Museum 4568) figured by Kuss (1965, p. 115).

A distal left humerus (F:AM 25421) from Morava Ranch Quarry is considerably larger than the largest known humerus of *D. superbus* (fig. 11). Greatest transverse width of the distal humerus is 72 mm. measured from the lateral to medial epicondyle. This can be compared to a measurement of 57–58 mm. for *D. superbus* (fig. 11). A complete humerus (CM 2400)



FIG. 8. Lateral view of right edentulous lower jaw, (F:AM 25423), (?)*Ysengrinia* sp., Harrison Formation, Morava Ranch Quarry, Box Butte County, Nebraska. $\times 0.5$.

described by Peterson, which I refer here to (?)*Ysengrinia*, measures 96 mm. between the epicondyles. It measures 302 mm. in total length (most proximal part of the lesser tuberosity to the distal extremity of the trochlear ridge), and so the Morava Ranch Quarry humerus would have an estimated length of about 225 mm. if proportions were similar, longer than any known *D. superbus* humeri.

A proximal phalanx (F:AM 25433) from Morava Ranch Quarry is tentatively referred to (?)*Ysengrinia* on the basis of size. It is much larger than similar phalanges of *D. superbus* (fig. 9) and could represent the same individual as the edentulous lower jaw, isolated M^1 , and distal humerus. Because it is a carnivore phalanx and the amphicyonid is the only large carnivore of this size known from the quarry, it probably belongs to that animal. Greatest length is 36.3 mm., greatest width across the base of the distal condyles is 13.6 mm.

A complete left humerus (CM 2400) from the Whistle Creek area initially described by Peterson (1910) measures approximately 300 mm. in length, equaling in size some of the largest living ursids (fig. 12). The

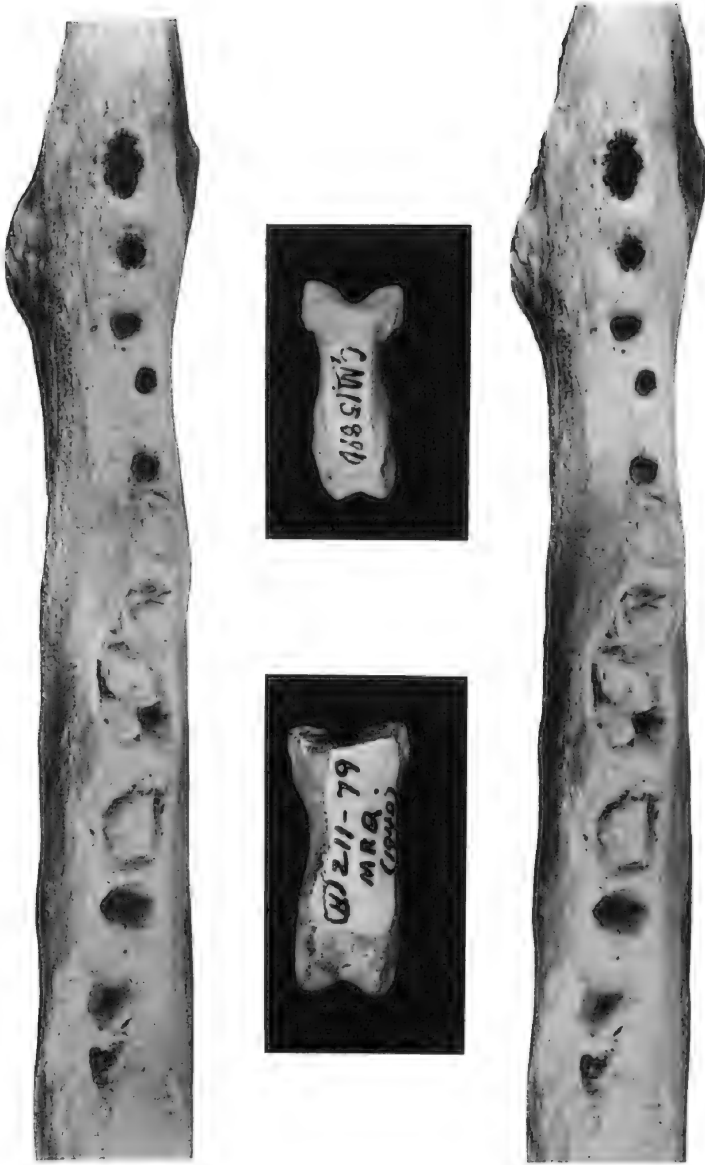


FIG. 9. Stereophotograph of the alveolar border of edentulous lower jaw (F:AM 25423), (?) *Ysengrinia*, Harrison Formation, Morava Ranch Quarry, Box Butte County, Nebraska. Center top, proximal phalanx of *Daphoenodon superbus* (CM 1589D), Harrison Formation, Quarry 3. Center bottom, proximal phalanx of (?) *Ysengrinia* sp. (F:AM 25433), Harrison Formation, Morava Ranch Quarry. All $\times 1.0$.

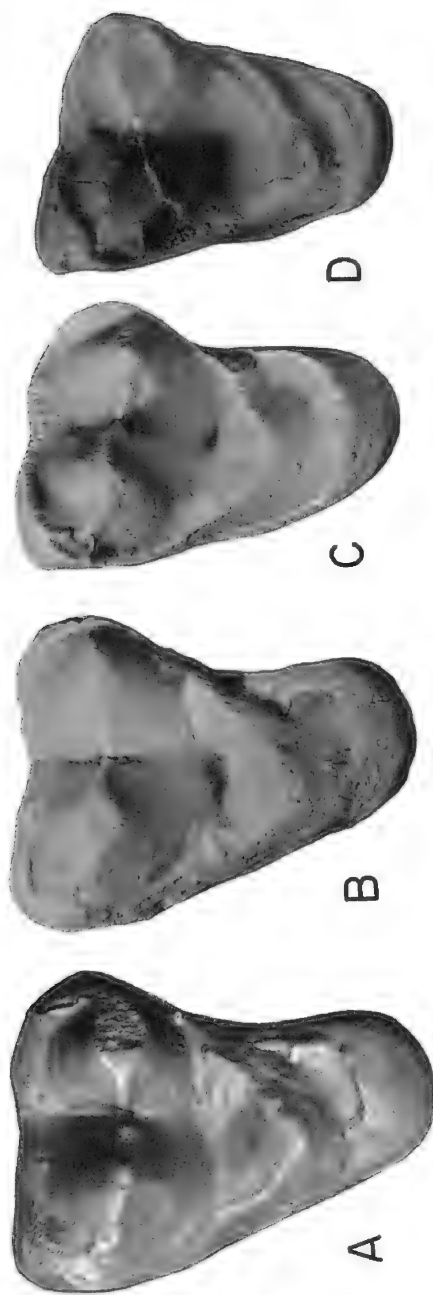


FIG. 10. A. F:AM 25420, (?) *Ysengrinia* sp., Harrison Formation, Morava Ranch Quarry, Box Butte County, Nebraska, occlusal view of M¹. B. AMNH 81049, (?) *Ysengrinia* sp., Harrison Formation, American Museum-Cook Quarry, Sioux County, Nebraska, occlusal view of M¹. C. AMNH 81048, *Daphoenodon superbus*, Harrison Formation, American Museum-Cook Quarry, Sioux County, Nebraska, occlusal view of unworn M¹. D. AMNH 81050, *Daphoenodon superbus*, Harrison Formation, American Museum-Cook Quarry, Sioux County, Nebraska, occlusal view of worn M¹. All $\times 2.0$.

form of the humerus and also the scars of muscles indicate that the function of the upper arm was much like that of living ursids, and the Giant Panda, *Ailuropoda* Milne Edwards. Muscle scars on the amphicyonid humerus are almost identical in extent and location with those depicted by Davis (1964, pp. 92, 93) in his study of the musculoskeletal system of the Giant Panda, and Davis's study serves as an excellent standard of comparison. In the amphicyonid the extensors and flexors of the forearm on the upper arm must have been well developed as in the panda: flexor and extensor surfaces of the distal humerus are expanded and deeply scarred by muscle attachments (lateral and medial epicondyles and the supracondylar ridges dorsal to the epicondyles).

In the panda studied by Davis and in mammals in general, the lateral epicondyle is the origin of major extensors of the wrist and digits (lateral and common superficial digital extensors, ulnar carpal extensor). This area shows massive scars and bony tuberosities in the amphicyonid similar to those in the panda, and a similar development of the extensor musculature can be inferred. Dorsal to the lateral epicondyle runs the lateral supracondylar ridge. In the panda the ridge forms the origin of the short head of the brachialis muscle behind which originates the long and short radial carpal extensors. Radial carpal extensors extend the wrist; brachialis is a major flexor of the forearm on the upper arm. The massive bony development of the supracondylar ridge above the lateral epicondyle in the amphicyonid parallels in detail the structure of the panda humerus. Among living Carnivora, the brachialis of the panda is unusual in that it has two heads, a long head innervated by the radial nerve and a short head supplied by the musculocutaneous nerve.¹

In the panda the short head of brachialis arises from the lateral supracondylar ridge with the long head arising from the deltoid ridge. Scars on the amphicyonid humerus show an indentation in the lateral supracondylar ridge at the point at which the short head of the brachialis takes its origin in the panda. Although the scar is probably the site of origin of a lateral collateral ligament of the elbow joint, the brachialis could have been anchored to the humerus immediately above the ligament as in *Ailuropoda*. It is highly probable that the amphicyonid also had a two-headed brachialis, a condition not indicative of special relationship but more likely of persistence of a primitive arctoid brachialis.

Medial epicondyle and medial epicondylar ridge of the distal humerus

¹ Both heads probably persist in the Lesser Panda (*Ailurus* Cuvier) but are fused together, based on double innervation of the brachialis by the radial and musculocutaneous nerves (Davis, 1964).

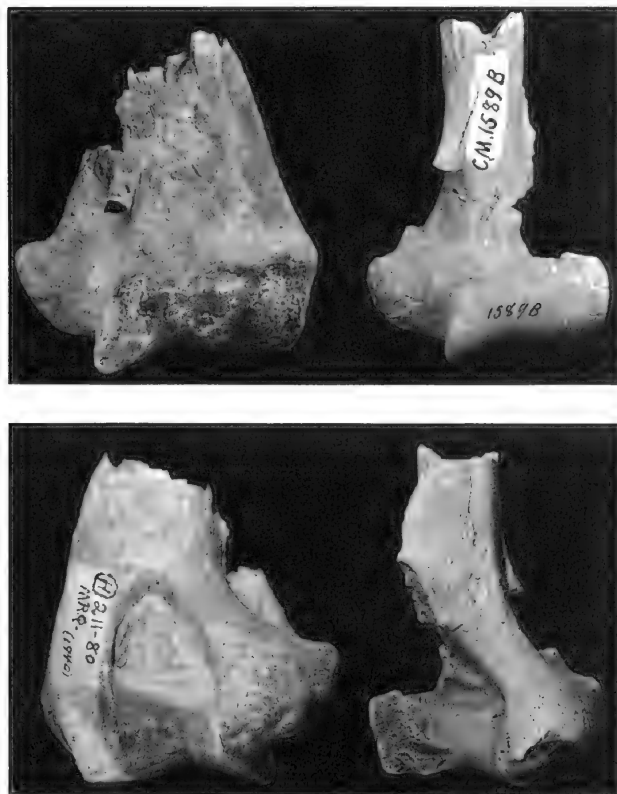


FIG. 11. Anterior and posterior views of a distal humerus of (?)*Ysengrinia* sp. (F:AM 25421), left, Morava Ranch Quarry, Box Butte County, Nebraska, compared with the largest known humerus of *Daphoenodon superbus* (CM 1589B), right, Quarry 3, Sioux County, Nebraska. $\times 0.5$.

are surfaces of origin for flexor muscles of the wrist on the forearm and are also similar in anatomy in both panda and amphicyonid. The medial epicondyle is a massive tuberosity pitted by deep muscle scars of the flexor group (deep digital flexors, ulnar carpal flexor, radial carpal flexor). The superior part of the epicondyle is enlarged in both mammals for the pronator teres. Because the remaining pronator of the mammalian forearm, pronator quadratus, lies between distal radius and ulna, its action or size cannot be determined in the amphicyonid.

Supination in the mammalian forearm is accomplished by the biceps brachii and the supinator. The biceps was large in the amphicyonid based on the deep, wide bicipital groove of the proximal humerus. Supinator was probably well developed as well. In mammals the supinator runs

between the lateral epicondyle of the humerus and the proximal shaft of the radius. In the panda, however, the supinator arises not from bone but from a ligamentous complex attached to the proximal radius and ulna and to the lateral epicondyle of the humerus. A lateral collateral ligament attaches the supinator to the lateral epicondylar ridge. The attachment of a similar ligament to the amphicyonid humerus may be represented by an elliptical scar on the ridge. The base of the scar lies about 20 mm. above the distal termination of the ridge; length of the scar is about 21 mm. It is deep and well marked in the amphicyonid and it is difficult to conclude that it could be for anything other than the lateral collateral ligament. Immediately above it would be the origin of the short head of brachialis. This interpretation suggests a large supinator muscle as in the panda and coupled with the evidence of a large pronator teres implies that supination and pronation were attended by powerful musculature in the amphicyonid.

The shaft of the amphicyonid humerus exhibits massive crests and ridges for muscles of adduction and abduction of the upper arm: fore-aft motion of the upper arm is certainly not the predominant function as in living canids. Total length of the humerus (CM 2400) is approximately 300 mm. of which the deltoid and pectoral crests occupy 200 mm. The inferior 65 mm. of this 200 mm. of deltoid crest is in the form of a prominent ridge which, if anatomy of the panda can be used as a guide, indicates a line of attachment between a well-developed brachialis (long head) and cephalohumeralis muscle (clavodeltoid and clavotrapezius according to Davis, 1964, p. 167). The cephalohumeralis, chief extensor of the foreleg in the panda, is undoubtedly indicated in the amphicyonid by virtue of identical muscle scars. In addition, Davis noted that the cephalohumeralis fibers insert "into the lower half of the deltoid ridge and the area between this ridge and a second ridge midway between the deltoid and pectoral ridges." Such a second ridge is also present on the amphicyonid humerus. Finally, the size and length of the pectoral ridge in the amphicyonid suggest a large pectoral muscle complex as in ursids and *Ailuropoda*. The smaller muscles of the humeral shaft of the panda can only be inferred in the amphicyonid on the basis of the overall similarity in anatomy to the panda upper arm. No obvious scars for the smaller muscles are present (e.g., acromiodeltoid, teres major, latissimus dorsi).

Prominent muscle scars at the proximal head of the amphicyonid humerus approximate those of the panda. These include the supraspinatus superiorly, the infraspinatus laterally, triceps posteromedially and posteriorly, and subscapularis medially. There is no large scar for teres minor either in amphicyonid or panda. The size and location of the triceps scars



FIG. 12. Anterior, lateral, and posterior views of complete left humerus (CM 2400) of (?) *Ysengrinia* sp., from a quarry 8 to 10 miles east of the Agate Spring Quarries, near the mouth of Whistle Creek, Sioux County, Nebraska, Harrison Formation, compared with similar views of distal left humerus (F:AM 25421) of (?) *Ysengrinia* sp., Morava Ranch Quarry, Box Butte County, Nebraska, Harrison Formation. Size difference is interpreted as sexual dimorphism. $\times 0.3$.

leads to the conclusion that this extensor of the forearm was similarly developed in panda and amphicyonid. Most prominent is the deep, massive depression on the posterior face of the proximal humerus for the origin of triceps medialis (long head). According to Davis (1964, p. 176), this is the smallest of the three heads of the panda triceps; the scar in the amphicyonid fits his description well. The major head of the triceps (triceps longus) attaches to the ventral border of the scapula so its size in the amphicyonid is not known.

The "rotator cuff" musculature of panda and amphicyonid is characterized by large infraspinatus and subscapularis muscles, in addition to a well-developed supraspinatus. Infraspinatus and subscapularis are the principal lateral and medial rotators of the upper arm, respectively. In contrast, the teres minor of the panda is a relatively small muscle, hardly differentiated from infraspinatus. Tendons of insertion of these rotator cuff muscles reinforce the capsule of the shoulder joint as well. Supraspinatus according to Davis functions as an extensor of the upper arm on the scapula as well as a lateral rotator.

In summary, the anatomy of the amphicyonid humerus shows detailed correspondence of scars, ridges, and crests to humeri of living ursids and the Giant Panda *Ailuropoda*. A similar musculature can be confidently inferred on this basis and probably a similar function of the upper forelimb. Powerful extension and flexion of the forelimb was coupled with a pronounced capability for abduction-adduction. Certain large rotator cuff muscles were predisposed toward stability of the scapulohumeral joint and could have effected powerful rotation of the humerus about its long axis. Ligaments of the joints no doubt restricted these actions and must remain an unknown factor. Yet it seems probable that locomotion of this amphicyonid must have been similar to the ambulatory gait of pandas and true bears. This allows (?) *Ysengrinia* to be distinguished from *Daphoenodon superbus* because the structure of the humerus of *Daphoenodon* is trending toward that of living canids, rather than ursids, and is suggestive of a more cursorial habit.

A right metacarpal V (CM 1897) from the University of Nebraska Quarry also is anatomically similar to this bone in ursids and *Ailuropoda*. The fifth is the largest and most massive of the metacarpals within the arctoid carnivores, according to Davis. Greatest length is 63.1 mm., greatest width of the distal end is 19.5 mm. Without doubt this metacarpal is of the stout, shortened type found in ursid-like carnivores of ambulatory gait and is not the slender elongate fifth metacarpal of cursorially adapted forms such as living canids (fig. 13).

The calcaneum (CM 2211) found by O. A. Peterson on the dump heap



FIG. 13. Dorsal and medial views of right fifth metacarpal (CM 1897) of (?) *Ysengrinia*, found by Peterson at University Hill in 1904, Harrison Formation, Sioux County, Nebraska. $\times 1.0$.

of the American Museum-Cook Quarry has a gross structure more like that of *Ailuropoda* than like species of the genus *Ursus* Linnaeus (fig. 14). Greatest length of the bone is about 90 mm., transverse width at the level of the sustentaculum and measured perpendicular to the long axis of the bone is about 45 mm. Davis regarded the tarsus of the panda as more primitive than that of *Ursus* and I would concur in this, noting that the similarity between the panda and amphicyonid calcanea is due to the primitive structure of the tarsus of both forms. Very likely the differences between calcanea of *Ailuropoda*-(?) *Ysengrinia* on one hand and *Ursus* on the other is directly related to the larger size of species of *Ursus*. Increase in width of tarsal bones in ursids is probably correlated with increase in size and weight. Davis appreciated this when he called attention to the fact that the breadth of the cuboid within *Ursus* is correlated with the absolute size of these bears (Davis, 1964, p. 120). Large pandas and large amphicyonids therefore could be expected to show broadening of the tarsal elements because of the additional weight which the tarsus must support. Thus the similar calcanea of *Ailuropoda* and the amphicyonid are interpreted as the result of similar weight and size coupled with retention of a primitive arctoid foot.

DISCUSSION: In his monograph on the Miocene Carnivora of western



FIG. 14. Anterior, medial, and posterior views of right calcaneum (CM 2211), (?) *Ysengrinia*, found by Peterson in 1908 on the quarry dump heap of the American Museum-Cook Quarry, Harrison Formation, Sioux County, Nebraska. $\times 0.8$.

Nebraska, Peterson (1910, p. 262) reported that a large canid of undetermined species, distinct from *Daphoenodon superbus*, was present in the Harrison Formation of Nebraska. Peterson's conclusion was based on a large humerus (CM 2400), a calcaneum (CM 2211), and a fifth metacarpal (CM 1897). Little is known of the locality which produced the humerus except that it was found "in the lower Harrison beds on Whistle Creek, Sioux County, Nebraska, about eight [to] ten miles east of the Agate Spring Fossil Quarries." Taken literally, this locality could lie within an area from the E 1/2, sect. 12, T. 28 N, R. 54 W, through sect. 7-8, T. 28 N, R. 53 W. This encompasses a low east-west trending ridge in which is probably situated the site of Peterson's quarry. Although the location remains unknown, it probably lay in the west end of the ridge immediately east of the junction of Whistle Creek with the Niobrara River.

On the other hand, the site at which Peterson discovered the fifth metacarpal can be located with certainty. As noted earlier, on August 9, 1904, Peterson explored University Hill and Carnegie Hill for the first time and found a few bones in the surface talus at University Hill. A field label in Peterson's hand indicates that one of the bones picked up on the surface was the fifth metacarpal of his "large canid." In 1905, E. H. Barbour opened the Nebraska State University Quarry at University Hill at or near the spot where Peterson obtained these fragments. Fossils obtained in the quarry constitute a significant part of the classic late Arikareean Agate Spring Quarries faunal assemblage, thus the occurrence of the metacarpal at the site shows that the amphicyonid was part of this fauna.

Peterson reported that the calcaneum came from "the edge of a quarry operated by the American Museum one mile north of the Agate Spring Quarries in the Harrison Formation." I have designated this locality the American Museum-Cook Quarry for reasons presented in the Addendum. Peterson apparently obtained only a few incidental specimens from this site on a brief visit in 1908.

Based on the complementary morphology of humerus, metacarpal, and calcaneum, the presence of a large bearlike ambulatory amphicyonid can be inferred in the late Arikareean fauna of Sioux County. Although Peterson thought that this material represented a canid, no canids of this size are known before the appearance of the large borophagine dogs (*Aelurodon* Leidy) in the Clarendonian of North America. A more complete picture of this large amphicyonid is based on additional material discovered by Ted Galusha in 1940 from the Harrison Formation, Morava Ranch Quarry, NE 1/4, sect. 6, T. 28 N, R. 52 W, Box Butte County, Nebraska. This quarry lies about 16 miles east of Peterson's localities. Included are the edentulous lower jaw (F:AM 25423), isolated M¹ (F:AM

25420), distal humerus (F:AM 25421), and proximal phalanx (F:AM 25433). The various elements from Morava Ranch Quarry could belong to a single individual on the basis of size, although there is no proven association of material.

It is improbable that Peterson's "canid" is referable to *Amphicyon* Lartet as currently defined by Kuss (1965, p. 22) or Ginsburg and Telles-Antunes (1968). In Europe the genus first appears in the early Burdigalian deposits of Wintershof-West, Bavaria, and Neuville and Chilleurs-aux-Bois, France.



FIG. 15. Lateral (left) and occlusal (right) views of M_1 , *Daphoenodon superbus* (CM 1589A), Agate Spring Quarry 3, Sioux County, Nebraska. $\times 2.0$.

This seems to be approximately contemporaneous with the first North American appearance of *Amphicyon* in the medial Hemingfordian Running-water Formation of Nebraska (Hunt, ms). These early species of *Amphicyon* are slender jawed, and in this and other features are distinguished from the deep, short Morava Ranch Quarry mandible (F:AM 25423). As the postcranial anatomy differs little from that of *Amphicyon*, the short, deep, and massive lower jaw becomes a key element in diagnosis.

Deep-jawed amphicyonids similar to the Morava Ranch Quarry carnivore are known from Stampian through Pontian deposits in Europe.¹ They have been placed in the genera *Brachycyon* Filhol, 1873 (Ginsburg, 1966, pp. 37–50), *Pseudocyon* Lartet, 1851 (Kuss, 1965, pp. 104–119; Ginsburg, 1961, 1967), and *Ysengrinia* Ginsburg, 1965 (Ginsburg, 1965, 1966). Known postcranial remains of the three genera are similar to those of *Amphicyon*

¹ The term "deep-jawed" refers to the fact that the lower jaw is about as deep below P_2 as below M_1 , resulting in a rectilinear ventral border of the mandible.

thus explaining the similarity of postcranial bones of Peterson's "canid" to the corresponding elements of *Amphicyon*.

Brachycyon: Ginsburg (1966), the most recent student of the genus, placed in it three lower jaws from Quercy, and a fragmentary skull, lower jaw, and partial hind limb, all of the same individual, from the Stampian Argiles des Milles, near Marseille (Bouches-du-Rhone), France. The genus is restricted to the Oligocene of France, and includes a single species, *Brachycyon palaeolycos* (Gervais). It was possible to compare casts of the holotype lower jaw of *Brachycyon* and a referred lower jaw from Quercy with the Morava Ranch Quarry mandible. *Brachycyon* is structurally similar in jaw form and in spacing and proportions of the alveoli, but is a much smaller carnivore. By enlarging the dimensions of the mandible and dentition, *Brachycyon* could give rise to the Morava Ranch Quarry amphicyonid as well as other deep-jawed amphicyonids of the Aquitanian of Europe.

Pseudocyon: Most European deep-jawed amphicyonids have been referred to *Pseudocyon* at one time or another. The type species of the genus, *Pseudocyon sansaniensis* Lartet, is based on a well-preserved lower jaw and dentition from the medial Helvetian of Sansan, Aquitaine Basin, France (Ginsburg, 1961, pl. 5). The genus has never been identified outside of Europe.

The most recently expressed viewpoints as to the taxonomic status of *Pseudocyon*, those of Kuss (1965) and Ginsburg (1961, 1967), are not entirely in agreement. Ginsburg initially included Aquitanian and Burdigalian amphicyonids in *Pseudocyon*: "*Pseudocyon* is a rare form known not only from the Vindobonian of Sansan, from Rimbez, from Ponsan-Soubiran and from Steinheim [*P. sansaniensis*], but also in the Burdigalian of Chilleurs-aux-Bois [*P. depereti* Mayet] and at St.-Gerand-le-Puy [*P. gerandianus* Viret]. This genus which is very similar to *Amphicyon* must share a common ancestry with it during the Stampian." Later Ginsburg modified his viewpoint to exclude the Aquitanian and early Burdigalian species (*P. gerandianus*, *P. depereti*) from Chilleurs-aux-Bois and St.-Gerand: "*Pseudocyon sansaniensis* is only known with certainty in the late Burdigalian of Pont-Pourquey (cf. Roman, 1923), in the Helvetian of Ponsan-Soubiran, of Sansan, as well as in the Tortonian of Steinheim (cf. Helbing, 1929) and, with still some doubt, in the Pontian of Gau-Weinheim (cf. Kuss, 1965, p. 137, fig. 85). The other remains attributed by Kuss (1965) to *Pseudocyon sansaniensis* are to me either uncertain or related to *Amphicyon*."

Kuss (1965) took a rather broad view of *Pseudocyon sansaniensis*, including in this single species Stampian, Aquitanian, and Burdigalian amphicyonids presumably ancestral to the holotype from Sansan. Ginsburg and Kuss

essentially agree on the composition of Helvetian and younger *Pseudocyon*, and include the holotype material from Sansan in this hypodigm, thus for the present *Pseudocyon sansaniensis* is best employed in the sense of Ginsburg (1967, p. 9). There is reasonable doubt that the Stampian, Aquitanian, and Burdigalian amphicyonids once referred to *Pseudocyon* are truly ancestral to that genus. Certain of these carnivores can be grouped in lineages which do not necessarily have a close relationship to *Pseudocyon*. This fact has been recognized by Ginsburg who has created the genus *Ysengrinia* for three species spanning a time period from the late Stampian of Le Cammas to the early Burdigalian of Chilleurs-aux-Bois.

Ysengrinia: Ginsburg (1965) created this genus because of a point demonstrated by Kuss: the upper dentition of *P. sansaniensis* (based on the only known associated upper and lower dentition from Ponsan-Soubiran) differs from the upper dentition referred to *P. gerandianus*. *Pseudocyon gerandianus* was morphologically similar in dentition to *P. depereti*. On this basis, Ginsburg removed *P. gerandianus* and *P. depereti* from *Pseudocyon* and placed them in the new genus *Ysengrinia*, later adding a third species, *Y. tolosana*, apparently based on Noulet's (1876) type lower jaw of *Amphicyon tolosanus* (Kuss, 1965, fig. 54) from the late Stampian of Le Cammas (Haute-Garonne, Aquitaine Basin).

Viret (1929) originally described "*P.*" *gerandianus* on the basis of a lower jaw with M_2 from the medial Aquitanian deposits at St.-Gerand. He referred a second lower jaw with P_2-M_1 to the species, and with reservation, a rostrum with P_2-M^2 . It is clear from Viret's discussion of these specimens that referral to *Pseudocyon* was based on the similarity of M_2 to that of *Pseudocyon sansaniensis*. Referral of the second lower jaw was based on the similarity of its M_1 to the M_1 of a referred species of *Pseudocyon*, *P. depereti*. The rostrum was simply tentatively placed with the lower jaws by Viret. Ginsburg, however, has accepted Viret's hypodigm of three specimens and has not questioned their association in a single taxon. He has based the species *Ysengrinia gerandiana* on the point that the upper molars of Viret's referred rostrum differ from the upper molars of the Ponsan-Soubiran *Pseudocyon sansaniensis*. This places rather excessive weight on the correct referral of the rostrum and lower jaws to a single species. It remains to be shown that the rostrum and lower jaws truly represent the same taxon. However, if the assumption is made that the *Y. gerandiana* hypodigm is validly associated, then it is significant that both Viret (1929, p. 124) and Ginsburg (1966) have noted the similarity to "*P.*" *depereti* Mayet, 1908, based on a lower jaw with M_{1-2} from the early Burdigalian deposits at Chilleurs-aux-Bois, France. *Ysengrinia gerandiana*, *Y. depereti*, and *Y. tolosana* Noulet, 1876, constitute Ginsburg's concept of *Ysengrinia*.

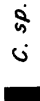






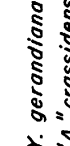



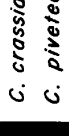


EUROPEAN MARINE INVERTEBRATE STAGE - AGE	WESTERN EUROPEAN LAND MAMMAL LOCALITIES	DESCRIBED RANGES OF CYNELOS, YSENGRINIA AND PSEUDOCYON
HELVETIAN AND YOUNGER -----	STEINHEIM SANSAN, PONSAN - SOUBIRAN ANJOU, RIMBEZ - SOS	 <i>C. sp.</i>  <i>P. sansaniensis</i>
BURDIGALIAN -----	PONT-POURQUEY LA ROMIEU CHILLEURS, NEUVILLE WINTERSHOF - WEST	 <i>C. helbingi</i>  <i>C. schlosseri</i>  <i>Y. dapereti</i>
LATE MEDIAL	CETINA DE ARAGON LAUNAC ULM (HASLACH - ECKINGEN - MICHELSBERGES)	 <i>"A." intermedius</i>  <i>Y. gerandiana</i>  <i>"A." crassidens</i>
AQUITANIAN EARLY -----	ST.-GERAND, MONTAIGU PAULHIAC WEISENAU PEU-BLANC, CODERET FLORSHEIM	 <i>C. rugosidens</i>  <i>C. lemanensis</i>  <i>Y. tolosana</i>
STAMPIAN	LE CAMMAS GARDOUCH ST.-HENRY QUERCY	 <i>C. crassidens</i>  <i>C. piveteaui</i>  <i>B. palaeolycos</i>

FIG. 16. Distribution in time of European species of *Brachycyon*, *Cynelos*, *Ysengrinia*, and *Pseudocyon*.

There is reason to believe that the type lower jaw of *Amphicyon robustus* Weitzel, 1930, from the early Aquitanian Cerithienschichten of Flörsheim¹ (Kuss, 1965, fig. 55) and the type lower jaw of *Amphicyon? astrei* Kuss, 1962, from the late Stampian of Gardouch (Haute-Garonne, Aquitaine Basin) (Kuss, 1962, figs. 2-3; 1965, fig. 72) can also be referred to *Y. tolosana*. Size and form of the dentition and depth of the mandible are criteria for referral (table 5). The probable ancestor of *Y. tolosana* is *Brachycyon palaeolycos* of the Quercy fissures. The latter is smaller, has less reduction of the premolars, and in other respects is an excellent morphological predecessor.

The teeth, jaws, and metacarpal described by Viret (1929) as *Amphicyon crassidens* Pomel (including the type specimen) from St.-Gerand could belong to the same species as *Ysengrinia gerandiana*. *Amphicyon crassidens* is a larger animal than *Y. gerandiana* (table 5), but given the frequent sexual dimorphism (cf. Ginsburg, 1961; Ginsburg and Telles-Antunes, 1968) of many amphicyonid species, the size differences may not be significant. Morphological differences between the two species are few. More important, however, in deciding the name of this sample, is the fact that the M¹ of *A. crassidens* (Viret, 1929, pl. 3) is morphologically similar to the type M¹ of *Amphicyon intermedius* Von Meyer, 1849, from the medial Aquitanian Süsswasserkalk of Michelsberg near Ulm (Kuss, 1965, fig. 75). It is possible that the St.-Gerand "A." *crassidens* and "P." *gerandianus*, as well as the Ulm "A." *intermedius* are names applied to the same large medial Aquitanian amphicyonid, the largest member of the family known up to this time. The name *A. intermedius* has priority; however, since these remains can be shown to differ sufficiently from those attributed to true *Amphicyon* (*A. major* Blainville, Sansan), another generic name is necessary. *Ysengrinia* will probably prove to be the preferred taxon if the St.-Gerand hypodigm is accepted as a single species. Kuss likewise recognized the identity of *A. intermedius* and *A. crassidens* but referred both to *Pseudocyon*.

It is to the species *Y. intermedia* as tentatively recognized here that the North American (?) *Ysengrinia* shows the closest correspondence. However, there are sufficient differences in M¹ structure and form of the fifth metacarpal among elements which can be compared to leave some doubt as to whether both can be referred to the same species. Since there must remain some doubt as well as to the validity of the genus *Ysengrinia*, I have designated the western Nebraska material as (?) *Ysengrinia* sp.

¹ Kuss also noted the resemblance between *A. tolosanus*, *A. robustus*, and *A.? astrei*. However, he did not place them in a common species in his revision of European amphicyonids (1965) and earlier denied (1962, p. 142) that the morphological resemblances between *A. tolosanus* and *A.? astrei* were significant.

TABLE 5
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER TEETH OF EUROPEAN SPECIES OF *Ysengrinia* COMPARED WITH
NORTH AMERICAN (?) *Ysengrinia* FROM THE HARRISON FORMATION OF WESTERN NEBRASKA
(All Measurements are of length, except $M_1W = M_1$ width. () = measurement based on alveolus.)

	P_3	P_4	M_1L	M_1W	M_2	C-M ₂	P_{1-4}
<i>Y. tolosana</i>	13	(20)	28.5	14-15	16.5	125	77
"A." <i>astrei</i>	—	16.5	(27)	13.9	(16)	—	—
"A." <i>tolosanus</i>	12	19	27	14	16	—	—
"A." <i>robustus</i>	—	—	—	—	—	—	—
<i>Y. intermedia</i>	—	—	—	—	—	—	—
"A." <i>crassidens</i>	14	20	31	16	—	—	—
	—	22	32	16.5	18	128	73
"P." <i>gerandianus</i>	—	—	24.3	—	16	127	69
	—	—	(27)	12	—	—	—
	—	—	—	—	16	105	—
<i>Y. depereti</i>	(12.5)	(14)	29	15	18	107	51
"P." <i>depereti</i>	(17.0)	(19.4)	(32.6)	—	(20)	(123)	(62.1)
(?) <i>Ysengrinia</i> sp.							Late Arikarean

Both *Cynelos* sp. and (?) *Ysengrinia* sp. from western Nebraska are in agreement in suggesting a correlation of the late Arikareean faunal assemblage of the Harrison Formation of Sioux and Box Butte counties, Nebraska, with early to medial Aquitanian faunal assemblages of France and Germany. Three lines of evidence suggest such a correlation: (1) (?) *Ysengrinia* sp. from western Nebraska, on the basis of mandibular and dental measurements, cannot be referred to the small pre-Aquitanian amphicyonid species; (2) dental measurements of *Cynelos* sp. from western Nebraska exclude referral to Burdigalian and later species, and in fact, the few late Aquitanian specimens of the genus are larger than the corresponding teeth of medial Aquitanian species and suggest that the molars are increasing in size in time accompanied by relative increase in size of the posterior molars relative to $P_4^1-M_1^1$. The third line of evidence is based on (3) stage of evolution of the amphicyonid dentition. Several lineages of amphicyonids undergo hypertrophy of $M_2^2-M_3^3$ relative to M_1^1 , resulting in a grinding dentition which parallels that of living ursids but which is arrived at by enlarging the rear molars in a manner different from that of the true bears. In North America the first such amphicyonids with hypertrophied dentitions appear in the Runningwater Formation of Nebraska (Hunt, ms). In Europe the first appearance of such forms is in the early Burdigalian of Chilleurs-aux-Bois and Wintershof-West (Kuss, 1965; Dehm, 1950). The late Arikareean fauna of the Harrison Formation contains amphicyonids without molar hypertrophy. The next younger stratigraphic unit in western Nebraska, the "Upper Harrison beds" of Peterson, also lacks amphicyonids with enlarged posterior molars. On this basis it seems that the Harrison-"Upper Harrison" deposits correlate with Aquitanian¹ deposits in Europe, whereas the Runningwater deposits must be approximately contemporaneous with early Burdigalian faunas such as Wintershof-West, Chilleurs-aux-Bois, and Neuville-aux-Bois (Ginsburg and Telles-Antunes, 1968). This conclusion is based entirely on the amphicyonid evidence. It is in broad agreement with correlation schemes recently proposed by Berggren (1969) and Wilson (1960, 1968).

Cynelos and (?) *Ysengrinia* also occur in the Bridgeport Quarries, Morrill County, Nebraska and (?) *Ysengrinia* is known from the "Upper Harrison beds" of Goshen County, Wyoming (Hunt, ms). Subsequent reports will deal with these specimens and their bearing on problems of correlation.

¹ Such terms have been employed in a broad context here for European continental rocks containing faunal assemblages called "Aquitanian" by European vertebrate paleontologists. The problem of correlation of the continental "Aquitanian" with the stratotype Aquitanian of the Aquitaine Basin, southern France, is recognized (see Vigneaux, 1971a, 1971b; Vigneaux and Marks, 1971).

Daphoenodon at present cannot be recognized in the European Tertiary. Without doubt its closest analogue is *Pseudocyonopsis* Kuss, 1965. *Daphoenodon superbus* resembles *P. ambiguus* (Filhol)-*P. quercensis* Ginsburg in dental features, but differences in dental proportions exist. *Daphoenodon superbus* was a moderately cursorial form. The only postcranial remains of *Pseudocyonopsis* do not appear to belong to a cursorial animal.

SUMMARY

In 1910 O. A. Peterson of the Carnegie Museum reported the occurrence of three species of carnivores in the Agate Spring Quarries, Harrison Formation, Sioux County, Nebraska: *Nothocyon annectens* (canid), *Paroligobunis simplicidens* (mustelid), and *Daphoenodon superbus* (amphicyonid). No new carnivores have been added to the fauna found in the quarries since these initial discoveries. Re-examination of fossils collected by Peterson from 1904 to 1910 led to the discovery of fragmentary remains of two additional species of amphicyonid carnivores which can be referred to the European genera *Cynelos* and (?) *Ysengrinia*. Although assignment to species is postponed until better material is acquired, it is suggested that the known material shows the greatest affinity to Aquitanian species in Europe, particularly to early and medial Aquitanian forms. A tentative correlation of the late Arikareean Agate Spring Quarries faunal assemblage is suggested with early to medial Aquitanian faunal assemblages of France and Germany on the basis of the amphicyonid evidence and is in accord with a recent proposal by Berggren (1969).

Two molars and a proximal radius of *Cynelos* from western Nebraska show it to be the smallest amphicyonid known from the quarries. Anatomy of the proximal radius indicates the carnivore was probably ambulatory in gait, much like one of the small species of living ursids.

Abundant remains of *Daphoenodon superbus* found in Quarry 3 allowed Peterson to unequivocally establish the skeletal anatomy of this carnivore. It proves to be a semicursorial animal of wolflike proportions; unpublished material of this genus demonstrates that several species became markedly cursorial.

Rare postcranial elements from various quarries in the Harrison Formation of Sioux County were described by Peterson (1910) as an indeterminate canid of large size. These included a large calcaneum, metacarpal, and humerus that are anatomically very similar to those of living ursids and the panda *Ailuropoda*. A smaller distal humerus of the same type was found at Morava Ranch Quarry in the Harrison Formation of Box Butte County to the east of Sioux County. The same quarry also produced an edentulous lower jaw, M¹, and proximal phalanx which probably

represent the same carnivore although there is no proven association of jaw, molar, phalanx, or distal humerus. These remains do not represent a canid as Peterson thought, but rather a large bearlike amphicyonid which is similar to European deep-jawed amphicyonids placed in *Ysengrinia*.

ADDENDUM

THE AMERICAN MUSEUM—COOK QUARRY

It is probable that (1) the quarry from which Peterson obtained the calcaneum (CM 2211) of (?) *Ysengrinia*, as well as (2) the quarry mentioned in the American Museum field records of 1908, and (3) the quarry described by Harold Cook in 1909 in a publication on various fossil carnivores from western Nebraska are one and the same site. This locality is designated the American Museum-Cook Quarry.

This conclusion is based on information in field records of 1908 of the American Museum (a field book entitled "Expeditions in Charge of Albert Thomson" includes notes of all American Museum expeditions to the Agate Quarries from 1908 to 1920, with records of a few incidental visits thereafter), the field labels of O. A. Peterson at the Carnegie Museum (no other field notes have been preserved), and on Cook's remarks in his publication of 1909.

In 1907 an American Museum field party made up of Albert Thomson, William Gregory, Paul Miller, and A. E. Anderson spent the last days of August in the vicinity of Agate, Nebraska, and collected three specimens from the Harrison and "Upper Harrison" deposits. This was the first entry of an American Museum field party into the Agate area.

In 1908 the American Museum sent a second expedition to the Agate area that included W. D. Matthew, Albert Thomson, William Stein, R. L. Moodie, and Harold Cook. The expedition worked a small quarry in the Harrison Formation which probably was discovered in the autumn of 1907 by Harold Cook. The assumption that Cook discovered the site, then took the American Museum party there in 1908, is based on a note in the American Museum field list of specimens for 1908 which reads: "No. 6. *Moropus*. Skull, parts of jaws, foot bones, vertebrae, etc. With jaws, teeth, and bones of *Rhinoceros*, *Amphicyon*, *Temnocyon*, *Parahippus*, etc.: All together in quarry. Lower Harrison. H. C. [Harold Cook] 1907. 4 mi. N.E. of Agate."

The critical reference is the mention of *Temnocyon* Cope. In a paper published in 1909 describing carnivores found in the Miocene beds of western Nebraska, Cook formally described the only *Temnocyon* material from Nebraska: "During the autumn of 1907 the writer was fortunate

enough to discover a 'pocket' of bones in the Lower Harrison beds, about two miles north of the Agate Spring Quarries [note that the American Museum records read 4 miles northeast of Agate postoffice], near Agate, Sioux County, Nebraska, and in probably the same horizon as these quarries. While the specimens so far obtained in this 'pocket' are generally more or less damaged or fragmentary, they represent a large variety of animals Among these are several species of Carnivora" Cook described two species of *Temnocyon*, which coincides with the American Museum notes of 1908 as to the presence of *Temnocyon* in the quarry. That this is the same *Temnocyon* in both the Cook publication and the American Museum field notes is probable because the specimens described by Cook (1909) are the only known *Temnocyon* from Nebraska.¹

The reference to *Temnocyon* in both Cook's paper and the American Museum's field records, and the additional reference to the discovery of *Temnocyon* with other mammals in a quarry or "pocket" seems to be compelling evidence suggesting that Cook's "pocket" and the American Museum quarry are the same site. In further support of this view, there is the fact that the American Museum and Cook's locality designations coincide: the American Museum field list records the locality as 4 miles northeast of Agate, whereas Cook (1909) gave the location as 2 miles north of the Agate Spring Quarries. When plotted on the Whistle Creek 1:125,000 topographic quadrangle, these locations turn out to be approximately the same place.

Furthermore, the American Museum-Cook Quarry appears to be the site at which Peterson obtained the (?) *Ysengrinia* calcaneum (CM 2211) in 1908, the same year that the American Museum party worked the quarry. He apparently collected the bone and other fragments late in August after the American Museum crew had departed for the season. Two field labels in Peterson's handwriting at the Carnegie Museum report the time of collection as "summer, 1908" or "Aug., 1908," and the horizon is given as "Lower Harrison beds, Miocene." One label reads "1 1/2 M. N. of Ag. Spr. Foss. Quar.," whereas the second label states "One mile

¹ All known specimens of *Temnocyon* from the Harrison Formation of Nebraska come from two localities: the American Museum-Cook Quarry, and "one-half mile west of Agate." Cook (1909) originally reported that the types of *Temnocyon venator* and *T. percussor* were found 1/2 mile west of Agate. However, Cook's personal catalogue of specimens records in his own handwriting that the type of *T. venator* was found 2 miles north of the Agate Spring Quarries (American Museum-Cook Quarry) whereas "one-half mile west of Agate" is still given as the locality of the type of *T. percussor*. All other remains of *T. percussor* other than the type come from the American Museum-Cook Quarry.

north of Agate Spring Fossil Quarries Sioux County Nebraska." Moreover, the first label reads, "This bone [calcaneum] was found on the dump of the quarry which the Am. Muse. party worked in 1908." The second label reads "This bone was found in a pile of fragments left on the edge of the quarry operated by the American Museum party. O.A.P." This evidence establishes a connection between Peterson's site of collection of the calcaneum and the American Museum quarry of 1908. The location given by Peterson corresponds with that given by Cook: the slight discrepancy in the distance north of the Agate Quarries is not serious in view of the loose method of designating collecting localities in the early twentieth century.

During final preparation of this report, Morris Skinner brought to my attention the correspondence between W. D. Matthew, Albert Thomson, and Henry F. Osborn during the field season of 1908, now filed in the Department of Vertebrate Paleontology, the American Museum of Natural History. Information in these letters definitely establishes that Cook's "carnivore pocket" (1909) and the American Museum quarry of 1908 are the same site. Matthew stated in a memorandum (undated) that "Material from the quarry discovered by [Harold Cook] in 1907 and opened up by the American Museum party in June 1908" comprises "No. 6 of the field catalogue of the expedition and includes a skull of *Moropus*." Later, in a letter dated June 25, 1908, to H. F. Osborn, Matthew said, "We worked in a quarry which Harold found last fall . . . and obtained a *Moropus* skull, better than any found yet, and a variety of carnivore, horse, rhinoceros, etc. jaws and teeth."

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